

Late Cenozoic Muricidae from Peru: Seven New Species and A Biogeographic Summary

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Abstract. Seven new species of muricid gastropods are described from late Cenozoic forearc deposits in Peru: *Carhuaspina comotrana*, gen. & sp. nov.; *Eupleura urbinai*, sp. nov.; *Muregina carlosmartini*, sp. nov.; *Muregina marijkeae*, sp. nov.; *Tactilispina vermeiji*, gen. & sp. nov.; *Trophon macharei*, sp. nov.; and *Phyllonotus*, sp. indet. Biogeographic and morphological comments are offered on four other muricids: *Acanthina katzi* Fleming, 1972; *Crassilabrum crassilabrum* (Sowerby, 1834); *Muregina lugubris* (Broderip, 1833); and *Xanthochorus cassidiformis* (Blainville, 1832). The late Cenozoic muricid fauna from southern Peru is characterized by a high proportion of toothed species, most belonging to a possible *Acanthina* clade; a high degree of endemism; and a few examples of immigrant taxa from predecessors of the modern tropical Panamic Faunal Province, with fewer from predecessors of the modern cold-temperate Magellanic Province.

INTRODUCTION

Five genera of endemic South American muricids with a Cenozoic fossil record in southern Peru (the ocenebrine genera *Acanthina* Fischer von Waldheim, 1807; *Chorus* Gray, 1847; and *Hermineospina* DeVries & Vermeij, 1997; the trophonine genus *Xanthochorus* Fischer, 1884; and the rapanine genus *Concholepas* Lamarck, 1801) have been reviewed recently (DeVries, 1995, 1997a, 2000, 2003, submitted; DeVries & Vermeij, 1997). Collectively, they account for most of the muricid species encountered in Miocene and Pliocene deposits in southern Peru. Patterns of muricid evolution and biogeography in Cenozoic forerunners of the Peruvian Faunal Province and the origin of the modern muricid fauna cannot be fully appreciated, however, until the remaining fossil muricid taxa are examined.

This paper describes additional muricid taxa from late Cenozoic beds of northern and southern Peru, including one new muricine and one new trophonine species, two new genera and species of toothed ocenebrines, and three new species of ocenebrines without a labral tooth. Further data are presented for several species previously described. Three rapanine species, *Stramonita biserialis* (Blainville, 1832), *Stramonita chocolata* (Duclos, 1832), and *Purpura boliviana* Philippi, 1887, as well as three undescribed species of *Stramonita*, are included in the analysis of the whole muricid fauna, even though an account of their fossil record in Peru has yet to be published.

GEOLOGY

The Cenozoic stratigraphy of the southern Peruvian Pisco and Sacaco forearc basins (Figure 1) was described by Muizon & DeVries (1985), Dunbar et al. (1990), and DeVries (1998). Uppermost Oligocene to middle Miocene fossiliferous sandstones in the Pisco Basin comprise portions of the Chilcatay formation. Upper Miocene and Pliocene bioclastic conglomerates and sandstones are assigned to the Pisco and La Planchada formations. A number of nearshore paleoenvironments are represented by the coarse-grained bioclastic sediments, including rocky intertidal cliffs and beaches, mixed sand-and-gravel attributed to high-energy shorefaces, low-energy embayments, and well-mixed lagoons.

Deposits of the Pliocene Taime formation in northern Peru were described by DeVries (1986, 1988). Most Taime sediments are thought to have been deposited on the inner shelf, nearshore and intertidally, and within a protected lagoon.

METHODS AND MATERIALS

Specimens described in this study were found by the author. Locality and sample descriptions are listed in the appendix. Lengths (L) and widths (W) are reported in millimeters. Dimensions of broken specimens are enclosed by parentheses. Types and figured specimens are deposited at the University of Washington's Burke Museum of Natural History and Culture in Seattle, Washington (UWBM), Ohio State University's Orton Museum in Columbus, Ohio (OSU), and the Departamento de Vertebrados, Museo de Historia Natural, Universidad de San Marcos, in Lima, Peru (MUSM INV).

Radiometric dates and biochronostratigraphic ages for

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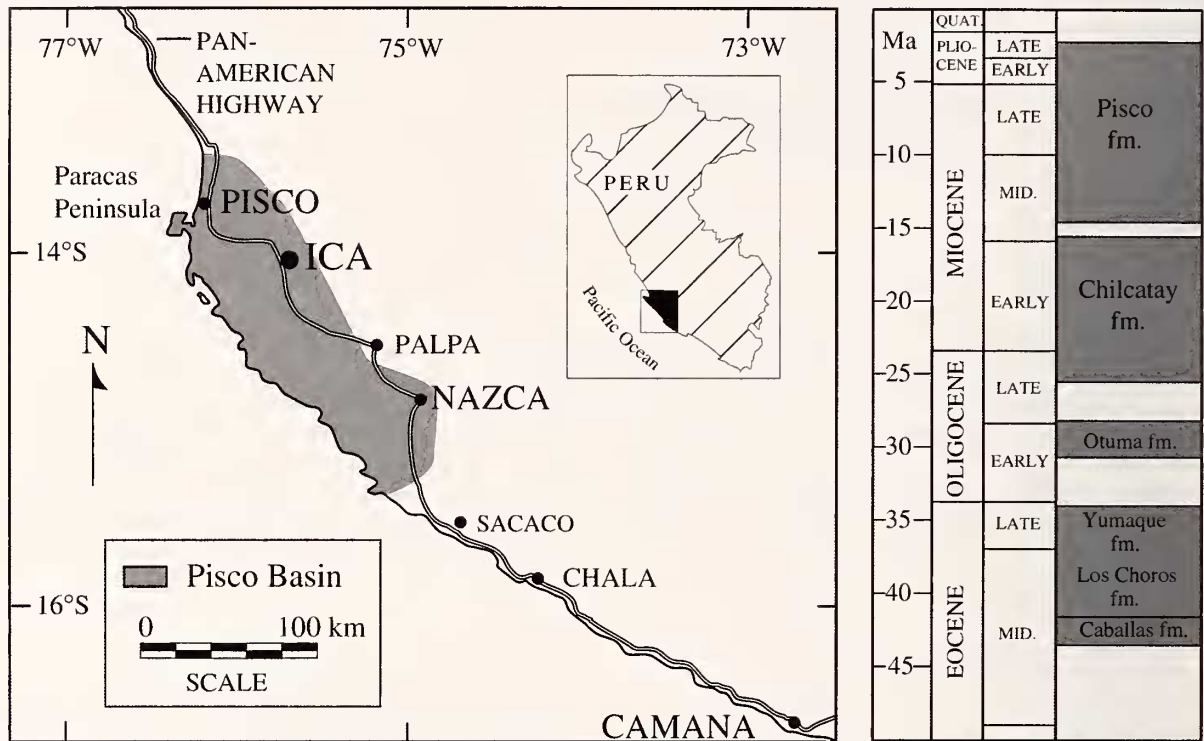


Figure 1. Location of the Pisco Basin in southern Peru and stratigraphy of Cenozoic marine sediments in the Pisco Basin. Stratigraphy based on Dunbar et al. (1990) and DeVries (1998).

deposits from the Pisco Basin and outcrops to the south are discussed by Dunbar et al. (1990) and DeVries (1998).

SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815

Subfamily OCENEBRINAE Cossmann, 1903

Genus *Acanthina* Fischer von Waldheim, 1807

Type species: *Buccinum monodon* Pallas, 1774.

Acanthina katzi Fleming, 1972

Figure 3

Acanthina crassilabrum katzi Fleming, 1972, in Watters & Fleming, 1972, p. 397, figs. 6m–6s.

Acanthina katzi (Fleming, 1972). DeVries & Vermeij, 1997, p. 613, figs. 2.13–2.15.

Acanthina katzi Fleming, 1972. DeVries, 2003, p. 342, figs. 59–67.

Discussion: Juvenile specimens from Lomas Chilcatay (Figure 2) constitute the first occurrence of *Acanthina katzi* in upper lower Miocene beds of Peru, with an age of about 18 Ma (DeVries, 1998). Other specimens had been found in older (latest Oligocene) and younger (middle Miocene) strata (DeVries, 2003).

The labral tooth on one Chilcatay specimen appears as a tongue-shaped extension on successive growth lines (Figure 3). The beginning of an enrolled labral tooth is embedded between the inner and outer shell layers at the margin of the outer lip.

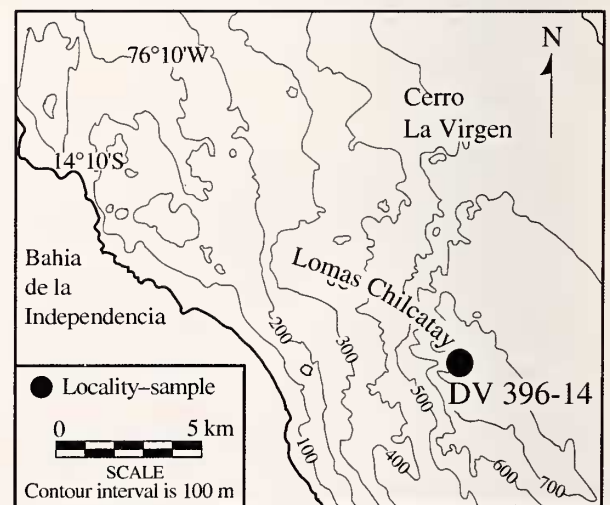


Figure 2. Map showing the locality-sample of juvenile *Acanthina katzi* and the type locality of *Carhuaspina comotrana*, gen. & sp. nov. (DV 396-14).

Material: (Both DV 396-14, early Miocene). UWBM 97605, L 8.8, W 6.6; MUSM INV 050, L (9.0) W (6.7).

Occurrence: Uppermost Oligocene to lower Miocene, southern Chile; and to upper middle Miocene, southern Peru.

Genus *Carhuaspina* DeVries, gen. nov.

Type species: *Carhuaspina comotrana*, sp. nov.

Diagnosis: Shell small, fusiform. Axial sculpture of regularly spaced weak swellings; spiral sculpture of about 30 undifferentiated spiral cords. Inner edge of outer lip dentate; labral tooth present. Siphonal canal short, open.

Description: As for type species.

Etymology: 'Carhuas,' a fishing outpost on Bahia de la Independencia and the coastal terminus of an abandoned road from Ica that passes by the type locality of *Carhuaspina comotrana*; and 'spina,' Latin noun for 'spine,' referring to the labral tooth.

Carhuaspina comotrana DeVries, sp. nov.

Figures 4–6

Diagnosis: As for genus.

Description: Shell less than 35 mm long; fusiform. Spire less than 25 percent, siphonal canal 15 percent of shell's length. Protoconch unknown. Teleoconch with at least four whorls. Sutures adpressed; shoulder barely angled; periphery midway between suture and anterior constriction. Axial sculpture of 12 evenly spaced faint swellings on each whorl. Spiral sculpture of about 30 low, rounded, smooth spiral cords, nearly uniform in size; cords separated by narrow grooves. Narrow infolding of shell surface at twentieth spiral cord from suture marked by aperturally pointed chevrons for last one-third turn of body whorl. Aperture elongate-oval; anal sulcus weak, with subsutural abaperturally reflected growth line. Columella missing. Outer lip prosocline, thickened, concavely beveled, with short labral tooth at outer edge at termination of exterior infolding. Inner edge of outer lip with five evenly spaced recessed teeth extending from just anterior to labral tooth posteriorly to suture; posteriormost two teeth weaker. Siphonal canal short, straight; siphonal fasciole thick, poorly preserved.

Discussion: The weak axial sculpture on this sole specimen of *Carhuaspina comotrana*, its labral tooth, and the dentate, beveled, inner edge of the outer lip (Figure 6) are features shared with members of the ocenebrine genus, *Acanthina*, including the contemporaneous *Acanthina katzi* (DeVries, 2003). The *Carhuaspina* specimen differs, however, in three important respects. It lacks differentiated spiral sculpture on all whorls, it has a labral tooth formed only from the outer shell layer, and it exhibits a

more pronounced abapertural subsutural reflection of an otherwise prosocline outer lip.

Carhuaspina comotrana might be considered a plausible transitional taxon between middle Miocene *A. katzi* and early late Miocene *Chorus frassinettii* DeVries, 1997. The differentiation of spiral cords on specimens of *C. frassinettii*, however, exceeds that of *C. comotrana*, and as is true for all examples of *Chorus*, specimens of *C. frassinettii* have an orthocline outer lip without dentition (except the labral spine), lack a subsutural reflection, and lack axial sculpture (DeVries, 1997a). The *Carhuaspina* specimen does resemble those of the Californian Pliocene ocenebrine, *Acanthinucella emersoni* Hertlein & Allison, 1959. Specimens of *A. emersoni*, however, have narrow, flat-bottomed interspaces between spiral cords, rather than the incised grooves of *Carhuaspina*, and lack a subsutural abapertural reflection.

Etymology: Comotrana, a western suburb of Ica and the inland terminus of an abandoned road from the fishing outpost at Carhuas. The road passes by the type locality of *Carhuaspina comotrana*.

Type locality: Lomas Chilcatay, southeast of the Comotrana-Carhuas road (locality-sample DV 396-14), in coarse-grained orange sandstone of the Chilcatay formation (Figure 2).

Material: UWBM 97606, DV 396-14, holotype, early Miocene, L 24.3, W 16.3.

Occurrence: Lower Miocene, southern Peru.

Genus *Muregina* Vermeij, 1998

Type species: *Murex lugubris* Broderip, 1833.

Muregina lugubris (Broderip, 1833)

Figures 7–9

Murex lugubris Broderip, 1833, p. 175.

Ocenebra lugubris Vokes, 1971, p. 67.

Ceratostoma lugubre (Broderip, 1833). Keen, 1971, p. 533, fig. 1033.

Ceratostoma lugubre (Broderip, 1833). Radwin & d'Attilio, 1976, p. 113, pl. 23, figs. 8–9.

Ceratostoma lugubre (Broderip, 1833). DeVries, 1986, p. 596, figs. 11, 13.

Muregina lugubris (Broderip, 1833). Vermeij, 1998, p. 858, figs. 1–12.

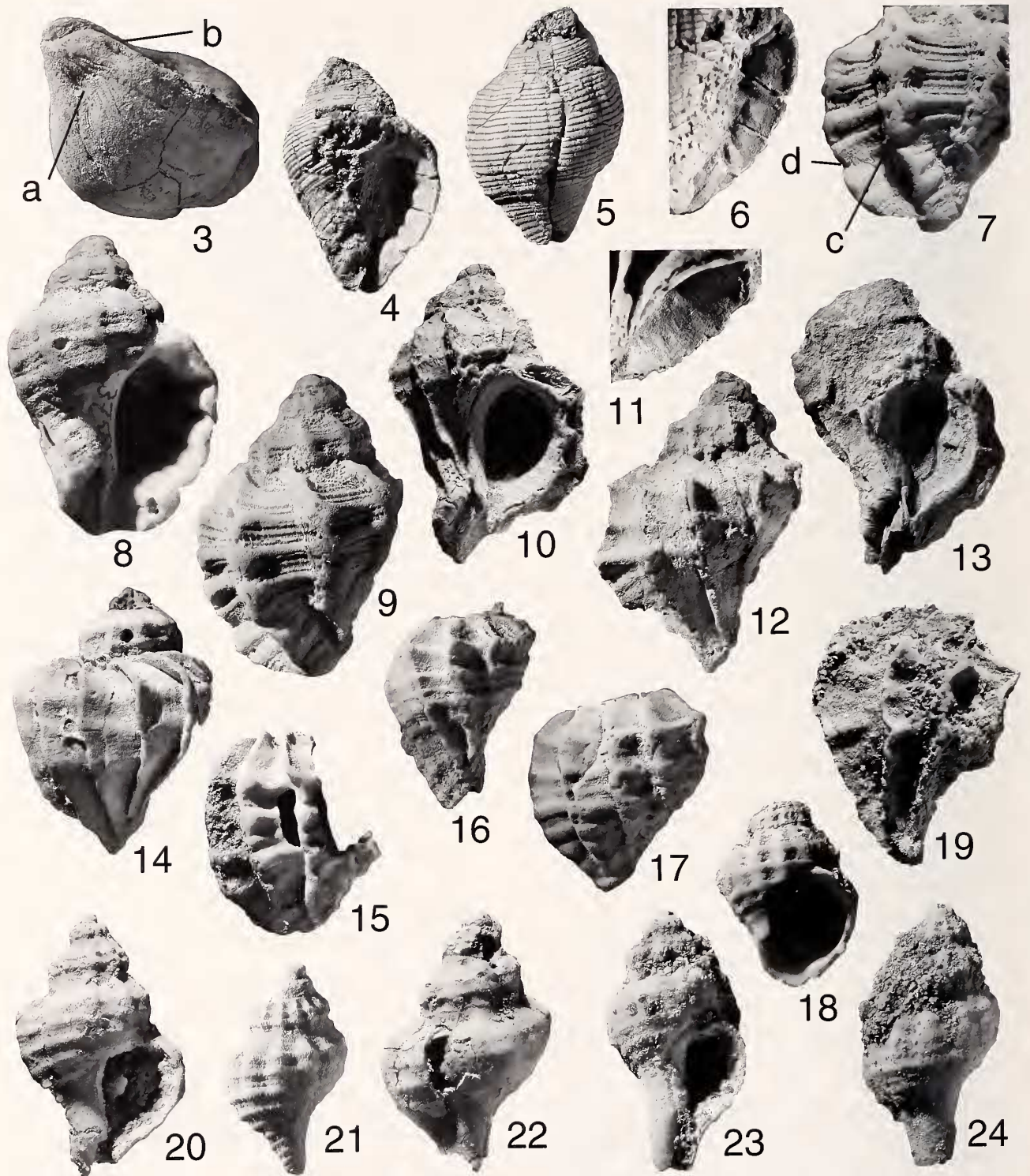
Murex fontainei Tryon, 1880, p. 126, pl. 35, figs. 384, 385.

Purpura fontainei (Tryon). Dall, 1909, p. 220.

Ceratostoma fontainei (Tryon, 1880). Keen, 1971, p. 533, fig. 1032.

Ceratostoma fontainei (Tryon). Alamo & Valdivieso, 1997, p. 50.

Discussion: A modern specimen of *Muregina lugubris* from Lobitos, northern Peru (OSU 37554; Figures 8, 9) has a small labral tooth arising from the fifth primary spiral cord from the suture (Figure 7), not from the ex-



ternal groove described by Vermeij (1998). *Fenolignum* Vermeij & Vokes, 1997, a late Oligocene ocenebrine from North Carolina, also has a labral tooth arising from a spiral cord and is, therefore, more similar to *Muregina* than once thought. Both genera have teeth inside the outer lip (Vermeij & Vokes, 1997; Vermeij, 1998). What best distinguishes *Muregina* from *Fenolignum* is the former's stubby biconic shape, which results from a well developed, planar, nearly horizontal sutural platform.

Material: OSU 37554, DV 211-21, Recent, L 27.5, W 19.0.

Occurrence: Recent, Costa Rica to Paita, Peru.

Muregina marijkeae, sp. nov.

Figures 10–13

Cerastostoma marijkeae DeVries, 1986, p. 595, pl. 35, figs. 8, 9, 12 (unpublished doctoral dissertation).

Diagnosis: Fusiform, with nine blade-like abaperturally flared varices on body whorl; sealed siphonal canal; no labral tooth.

Description: Shell about 35 mm long; fusiform. Spire 30 percent, siphonal canal 20 percent of shell length. Protoconch unknown. Teleoconch with at least four whorls. Shoulder weakly angulate; sutures impressed; sutural platform planar, weakly inclined. Periphery anterior to midpoint of aperture. Axial sculpture of nine bladelike abaperturally flared varices extending from suture to siphonal fasciole; varices weakly spinose at intersection with posteriormost three spiral cords; spines short, broad-

ly open. Spiral sculpture of three primary cords: first at shoulder, second at periphery, third halfway between first and second. Two to three weak primary cords on anterior half of whorl; two to three secondary spiral cords between primary cords. Aperture oval; anal sulcus barely perceptible. Columella smooth, inner lip adherent. Outer lip slightly prosocline, planar; anterior half of inside surface with five small recessed teeth. Labral tooth absent. Siphonal canal closed, twisted left, then right and slightly dorsally. Strong siphonal fasciole; pseudumbilicus broadly wedge-shaped.

Discussion: The two known specimens of *Muregina marijkeae* share with specimens of *M. lugubris* a similar spiral sculptural pattern, aperture, and closed siphonal canal, but differ by having more blade-like varices, less well developed spiral sculpture, and no labral tooth. The absence of a labral tooth could be considered a noteworthy difference at the generic level, but as observed by Vermeij (1998), *M. lugubris* might be the only member of its genus with a labral tooth, as is the case for *Jaton decussatus* (Gmelin, 1791), a late Pleistocene toothed species of the late Oligocene to Recent edentate *Jaton* Pusch, 1837 (Vermeij & Houart, 1996).

Etymology: Named for the author's wife, Marijke van Heeswijk.

Type locality: Southeastern rim of Quebrada Taime, south of El Alto (locality-sample DV 244-2), northern Peru (Figure 25). Two specimens were recovered from lagoonal siltstones of the Golf Course member of the Taime formation (DeVries, 1986, 1988).

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Figure 3. *Acanthina katzi* Fleming, 1972. UWBM 97605. Oblique anteriolateral view of the labral tooth expressed in growth lines on the surface of the body whorl (a) and embedded between the inner and outer shell layers at the margin of the outer lip (b). Specimen is 8.8 mm long.

Figures 4–6. *Carhuaspina comotrana*, gen. & sp. nov. UWBM 97606. Figure 4. Holotype, abapertural view. Length is 24.3 mm. Figure 5. Apertural view. Figure 6. Close-up of the labral tooth and dentition inside of the outer lip.

Figures 7–9. *Muregina lugubris* (Broderip, 1833). OSU 37554. Figure 7. Oblique view of anterior showing labral tooth passing through penultimate (c) and last varices (d). Length is 27.5 mm. Figure 8. Apertural view. Figure 9. Abapertural view.

Figures 10–13. *Muregina marijkeae*, sp. nov. Figure 10. OSU 37552. Syntype, apertural view. Length is 30.6 mm. Figure 11. OSU 37552. Close view of dentition inside the outer lip. Figure 12. OSU 37552. Abapertural view. Figure 13. OSU 37553. Syntype, apertural view showing fused siphonal canal. Length is 32.3 mm.

Figures 14–19. *Muregina carlosmartini*, sp. nov. Figure 14. UWBM 97607. Holotype, abapertural view. Length is 31.4 mm. Figure 15. UWBM 97608. Paratype, abapertural view of broken specimen. Length is 30.0 mm. Figure 16. MUSM INV 051. Paratype, abapertural view, spire is missing. Length is 22.3 mm. Figure 17. UWBM 97610. Paratype, abapertural view, spire is missing. Length is 22.4 mm. Figure 18. MUSM INV 054. Paratype, juvenile, apertural view, columella and siphonal canal are missing. Length is 13.5 mm. Figure 19. UWBM 97611. Paratype, lateral view of body whorl, obscured by matrix. Length is 32.0 mm.

Figures 20–24. *Eupleura urbinai*, sp. nov. Figure 20. UWBM 97621. Holotype, apertural view. Length is 22.1 mm. Figure 21. UWBM 97623. Paratype, abapertural view. Length is 12.4 mm. Figure 22. UWBM 97621. Abapertural view. Figure 23. UWBM 97622. Paratype, apertural view. Length is 20.9 mm. Figure 24. UWBM 97622. Abapertural view.

Material: Both DV 244-2, late Pliocene. OSU 37552, syntype, L 30.6, W 20.8; OSU 37553, syntype, L 32.3, W (21.3).

Occurrence: Upper Pliocene, northern Peru.

Muregina carlosmartini, sp. nov.

Figures 14–19

Diagnosis: Shell squatly fusiform, with eight to twelve lamellar varices, seven or eight primary spiral cords; no labral tooth.

Description: Shell to 45 mm long; squatly fusiform. Spire poorly preserved, about 25 percent of shell length; body whorl weakly constricted anteriorly, siphonal canal less than 20 percent of shell length. Protoconch unknown. Teleoconch with four to five whorls. Shoulder angulate; sutures impressed; sutural platform planar, moderately to steeply inclined. Whorls with eight to twelve rounded to lamellar varices, uniformly spaced, extending from suture to shoulder to siphonal fasciole; variably flaring adaperturally or recurved abaperturally at intersection of varices and spiral cords. Spiral sculpture absent from sutural platform; with seven sharply rounded primary cords between shoulder and siphonal fasciole; interspaces usually with medial secondary cord and one to two intervening tertiary cords separated by narrow grooves; spiral sculpture sometimes subdued or obsolete. Short spines produced at intersection of primary spiral cords and lamellar varices. Shape of aperture and columella unknown. Outer lip broad when terminal lamellae present but not thickened from within; possibly dentate within inner margin; labral tooth absent. Siphonal canal short, open. Siphonal fasciole slightly stronger than primary spiral cords.

Discussion: The axial and spiral sculpture on specimens of *Muregina carlosmartini* is like that on specimens of *M. lugubris*, except that all primary spiral cords on the former are about equally strong. Like specimens of *M. marijkeae*, those of *M. carlosmartini* lack a labral tooth.

Some specimens of *Muregina carlosmartini* from Sud-Sacaco intertidal bioclastic sandstones have sharper, adaperturally flaring lamellar varices and reduced spiral sculpture, especially on the body whorl. A specimen with an intermediate morphology (Figure 19) suggests that both phenotypes should be assigned to the same species.

Most specimens of *Muregina carlosmartini* were found in lower Pliocene beds (Muizon & DeVries, 1985) near Sacaco (Figure 26). The oldest specimen of *M. carlosmartini* (Figure 17) was found in a shell bank ringed basement rocks on the eastern side of Quebrada Riachuelo (Figure 50). Associated invertebrates from this shoreface deposit, particularly the muricids *Acanthina obesa* DeVries, 2003; *Hermineospina philippi* Mörnicke, 1896; and *Concholepas kieneri* Hupé, 1854, suggest a late Miocene age. Sandstones 50 meters lower in the section con-

tain a middle Miocene molluscan assemblage with *Anadara seclurana* Olsson, 1932, *Turritella infracarinata* Gryzbowski, 1899, and *A. katzi*. Shell beds from shell banks 20–30 meters higher in the section yield early Pliocene specimens of *Acanthina triangularis* DeVries, 2003, and *Hermineospina saskiae* DeVries & Vermeij, 1997.

Type locality: Sud-Sacaco (locality-sample DV 361-5) in beds flanking a depression on the west side of the Panamerican Highway (Figure 26).

Etymology: Named in memory of Carlos Martin, Sr., the late owner of a small farm and olive grove at Sacaco and once a tireless collector of fossil vertebrates.

Material: UWBM 97607, DV 361-5, holotype, early Pliocene, L (31.4), W 24.1; UWBM 97608, DV 360-1, paratype, early Pliocene, L (30.0), W (25.2); UWBM 97609, DV 360-1, paratype, early Pliocene, L (25.9), W (18.9); UWBM 97610, DV 1230-1, paratype, late Miocene, L (22.4), W (20.3); UWBM 97611, DV 361-10, paratype, early Pliocene, L (32.0), W (25.3); MUSM INV 051, DV 360-1, paratype, early Pliocene, L (22.3), W (16.7); MUSM INV 052, DV 362-1, paratype, early Pliocene, L (23.4), W (19); MUSM INV 053, DV 360-1, paratype, early Pliocene, L (28), W (19); MUSM INV 054, DV 1029-1, paratype, early Pliocene, L (13.5), W 10.2.

Occurrence: Upper Miocene to lower Pliocene, southern Peru.

Genus *Eupleura* H. & A. Adams, 1853

Type species: *Ranella caudata* Say, 1822, by subsequent designation, F. C. Baker, 1895.

Eupleura urbinai, sp. nov.

Figures 20–24

Diagnosis: Dorso-ventral compression not pronounced; two opposing varices rounded, weakly angled at shoulder.

Description: Shell less than 25 mm long; broadly fusiform, dorso-ventral compression not pronounced. Spire 50 percent, siphonal canal 20 percent of shell length; latter sharply constricted. Protoconch unknown. Teleoconch with four whorls. Sutures impressed, shoulder weakly angulate, sutural platform narrow, planar, steeply sloping. Periphery slightly anterior to shoulder. Axial sculpture of nine to eleven rounded ribs on early whorls; body whorl with two opposing varices and three low rounded intervening ribs. Spiral sculpture of six to eight primary spiral cords between shoulder and anterior end; second, third, and fourth cords more widely spaced; remaining posterior cords weakly developed. Interspaces with one to three secondary spiral cords. Aperture broadly oval. Parietal and columellar margins missing. Outer lip thickened as varix; inside edge with five to six round, evenly spaced.

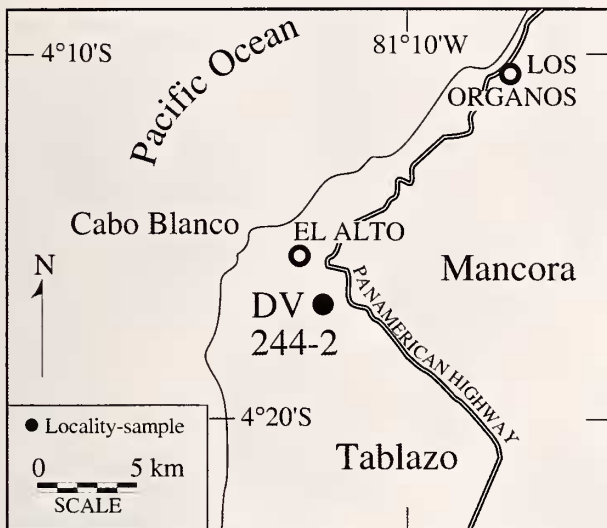


Figure 25. Type locality (locality-sample DV 244-2) of *Muregina marijkeae*, sp. nov.

bead-like teeth. Siphonal canal straight, open; slightly angled to left but not dorsally. Siphonal fasciole weakly arched; pseudumbilicus absent.

Discussion: Specimens of *Eupleura urbinai* are neither greatly compressed dorsoventrally nor are the varices alate. Thus, they differ from specimens of eastern tropical Pacific *E. muriciformis* (Broderip, 1833) (Pliocene to Recent; see Pilsbry & Olsson, 1941, and Vokes, 1989), *E. prenitida* Vokes, 1989 (Miocene), *E. nitida* (Broderip, 1833) (Recent), and *E. pectinata* (Hinds, 1844) (Miocene to Recent). Specimens of *E. urbinai* are even less sculptured than specimens of *E. thompsoni* Woodring, 1959, from the upper Miocene Gatun formation of Panama (see Woodring, 1959, and Vokes, 1989b). They most resemble specimens of *E. plicata* (Reeve, 1844), a species that presently ranges from Central America to northern Peru (G. Herbert, written communication, 2004). Specimens of *E. urbinai* have three intervarical ribs, however, rather than the five or six present on specimens of *E. plicata*.

Etymology: Named for Mario Urbina Schmidt, who has worked selflessly to advance the causes of vertebrate paleontology and paleontology students in Peru.

Type locality: Roadcut along the Panamerican Highway on the north side of the Yauca Valley (locality-sample DV 809-1) in a bioclastic sandstone horizon (Figure 26).

Material: UWBM 97621, DV 809-1, holotype, L (22.1), W 14.6; UWBM 97622, DV 809-1, paratype, L 20.9, W 11.3; UWBM 97623, DV 809-1, paratype, L 12.4, W 7.6. All early Pliocene.

Occurrence: Lower Pliocene, southern Peru.

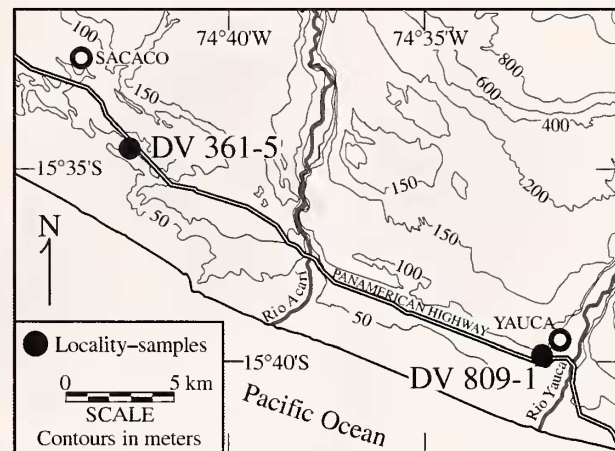


Figure 26. Type localities of *Muregina carlosmartini*, sp. nov. (locality-sample DV 361-5); *Eupleura urbinai*, sp. nov. (DV 809-1); and *Trophon macharei*, sp. nov. (DV 809-1).

Genus *Crassilabrum* Jousseau. 1880

Type species: *Murex crassilabrum* (Sowerby, 1834).

Crassilabrum crassilabrum (Sowerby, 1834)

Figures 27–35

Murex labiosus Gray, 1828, p. 4, pl. 6, fig. 9 (not *Murex labiosus* Wood, 1828).

Purpura crassilabrum Sowerby II, 1834, fig. 14.

Murex crassilabris Potiez & Michaud, 1838, p. 414, pl. 33, figs. 10, 11.

Crassilabrum crassilabrum Jousseau, 1880, p. 335.

Tritonalia crassilabrum Sowerby, Dall, 1909, p. 219.

Tritonalia crassilabrum (Gray), Herm, 1969, p. 91.

Crassilabrum crassilabrum (Sowerby, 1834), Marincovich, 1973, p. 33, fig. 70.

Crassilabrum crassilabrum (Sowerby, 1834), DeVries, 1986, p. 610, figs. 14, 15.

Crassilabrum crassilabrum (Sowerby), Alamo & Valdivieso, 1997, p. 54, fig. 138.

Crassilabrum crassilabrum (Sowerby, 1834), Forcelli, 2000, p. 89, fig. 236.

Discussion: The geographic range of *Crassilabrum crassilabrum* is herein extended for the late Pliocene, early Pleistocene, and middle Pleistocene from its modern northern limit of about 8°S (Alamo & Valdivieso, 1997) to 4°30'S, where it occurs in deposits of the Mancora and Talara tablazos (DeVries, 1986, 1988). In southern Peru, specimens occur at all subepochal intervals back to the late early Pliocene. No differences were noted between the youngest and oldest specimens. To date, no tricordate ocenebrines lacking a labral tooth that might plausibly be ancestral to *C. crassilabrum* have been found in lowermost Pliocene or upper Miocene deposits of Peru. A Miocene or early Pliocene *Crassilabrum* from Chiloe Island, southern Chile (Watters & Fleming, 1972), is misidentified; it may be an example of *Vitularia* Swainson, 1840,



or a related undescribed genus (G. Herbert, 2003, personal communication).

Material: MUSM INV 055, DV 465a-1, late Pleistocene, L 27.4, W 17.5; MUSM INV 056, DV 399-1, Recent, L 21.9, W 12.6; MUSM INV 057, DV 810-1, early Pleistocene, L (22.5), W 15.6; MUSM INV 058, DV 769-1, middle Pleistocene, L (22.4), W 16.6; MUSM INV 059, DV 1031-1, early late Pliocene, L (15.3), W (11.6); OSU 37543, DV 112, early to middle Pleistocene, L 29.7; OSU 37544, DV 191, late Pliocene, L 29.5; OSU 37545, DV 202, early Pleistocene, L (16.8), W 13.0; W (19); UWBM 97612, DV 1372-1, Recent, L 20.3, W 11.1; UWBM 97613, DV 923-1, late early Pliocene, L (17.5), W (8.1); UWBM 97614, DV 1418-1, late Pliocene, L (24.2), W 17.4; UWBM 97615, DV 1254-12, late Pliocene, L (12.2), W (6.6).

Occurrence: Lower Pliocene, southern Peru. Upper Pliocene, northern to southern Peru. Early Pleistocene, northern Peru to Chile. Recent: Southern Peru to Chile.

Tactilispina, gen. nov.

Type species: *Tactilispina vermeiji*, sp. nov.

Diagnosis: Eight to eleven axial ribs per whorl on posterior half of whorl; sometimes with short, recurved, hollow spines at shoulder; six primary spiral cords, fifth extended as spatulate tooth; elongate open siphonal canal.

Description: As described for species.

Etymology: 'Tactilis,' Latin adjective, 'able to be touched,' and 'spina,' Latin noun, 'spine,' named for the paleontologist Geerat Vermeij's ability to see a fossil with his fingers.

Tactilispina vermeiji, sp. nov.

Figures 36–49

Diagnosis: As described for genus.

Description: Shell about 35 mm long; fusiform. Spire 30 to 35 percent of shell length. Base of body whorl sharply constricted, siphonal canal moderately elongate, about 20 percent of shell length. Protoconch unknown. Teleoconch with four to five whorls. Shoulder angulate; sutures weakly impressed; sutural platform planar, weakly to moderately inclined. All whorls with eight to eleven axial ribs; ribs low across the sutural platform, well developed on posterior half of whorl, generally absent anterior to whorl's constriction. Spiral sculpture of six low rounded to steeply rounded primary spiral cords posterior to whorl's constriction. Anteriormost cord at shoulder, sometimes producing short, abaperturally and adaxially recurved hollow spines at intersection with axial ribs. Second anteriormost spiral cord at periphery; fifth cord extended through depression in varix or rib as bluntly rounded spatulate labral tooth. Sutural platform with eight low rounded to flattened secondary spiral cords. Two to four secondary cords between primary spiral cords, twelve to fourteen anterior to sixth primary cord; all secondary cords separated by narrow grooves; some cords bisected with narrow groove. Aperture oval. Anal sulcus barely perceptible; parietal area slightly excavated. Columella smooth, anterior portion of inner lip adherent. Outer lip with six low, oval, recessed teeth, each corresponding to an external primary interspace. Siphonal canal elongate, open to nearly closed, straight to slightly recurved left and dorsally. Siphonal fasciole arched; pseudumbilicus wedge-shaped.

Discussion: Specimens of *Tactilispina vermeiji* were found on the eastern slopes of the Rio Ica in channel

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Figures 27–35. *Crassilabrum crassilabrum* (Sowerby, 1834). Figure 27. MUSM INV 055. Apertural view. Length is 27.4 mm. Figure 28. UWBM 97613. Abapertural view of outer lip fragment. Length is 17.5 mm. Figure 29. MUSM INV 055. Abapertural view. Figure 30. UWBM 97612. Apertural view. Length is 20.3 mm. Figure 31. UWBM 97612. Abapertural view. Figure 32. MUSM INV 056. Apertural view. Length is 21.9 mm. Figure 33. MUSM INV 059. Abapertural view of broken specimen. Length is 15.3 mm. Figure 34. OSU 37545. Abapertural view of broken specimen. Length is 16.8 mm. Figure 35. MUSM INV 057. Abapertural view. Length is 22.5 mm.

Figures 36–49. *Tactilispina vermeiji*, gen. & sp. nov. t = labral tooth. Figure 36. MUSM INV 060. Paratype, abapertural view. Length is 29.4 mm. Figure 37. MUSM INV 060. Lateral view. Figure 38. MUSM INV 060. Oblique lateral view showing labral tooth extending through penultimate varix. Figure 39. UWBM 97616. Holotype, close view of dentition of inside of outer lip. Length is 27.3 mm. Figure 40. UWBM 97616. Apertural view. Figure 41. UWBM 97616. Abapertural view. Figure 42. MUSM INV 061. Paratype, abapertural view. Length is 24.8 mm. Figure 43. MUSM INV 061. Lateral view. Figure 44. MUSM INV 062. Paratype, oblique lateral view showing labral tooth extending through penultimate varix. Length is 23.5 mm. Figure 45. UWBM 97618. Paratype, apertural view, outer lip missing. Length is 11.0 mm. Figure 46. UWBM 97619. Paratype, lateral view of broken specimen. Length is 23.3 mm. Figure 47. UWBM 97617. Paratype, lateral view. Length is 30.0 mm. Figure 48. UWBM 97619. Oblique view of spire. Width is 14.0 mm. Figure 49. MUSM 063. Paratype, view of spire. Width is 14.4 mm.

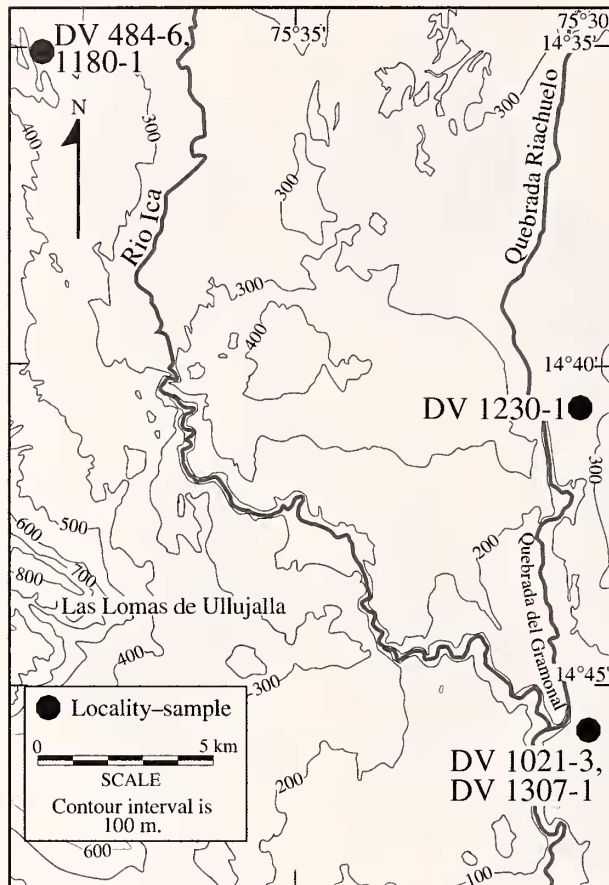


Figure 50. Type locality (DV 1180) of *Tactilispina vermeiji*, sp. nov., locality-sample (DV 1230-1) of oldest specimen of *Muregina carlosmartini*, sp. nov., and locality-sample (DV 484-6) of *Phyllonotus*, sp. indet. Other localities with *T. vermeiji* (DV 1021, 1307) are also noted.

deposits above Quebrada Gramonal and on the western slopes in a paleo-strandline deposit at the foot of Cerro Yesera de Amara (Figure 50). Associated mollusks at Quebrada Gramonal (*Turritella infracarinata*, *Ficus alemanae* DeVries, 1997, *Anadara sechurana*, *Acanthina katzi*) suggest a late middle Miocene age (DeVries, 1997b, c). The same middle Miocene assemblage at Yesera de Amara occurs about 20 meters above a horizon containing *T. vermeiji* with *Ficus distans* Sowerby, 1846; *Acanthina katzi*; *Olivancellaria tumorifera* (Hupé, 1854); and *Testallium cepa* (Sowerby, 1846). The occurrence together of the latter species suggest a latest early Miocene or early middle Miocene age (DeVries, 1998).

Specimens of *Tactilispina vermeiji* range from being fusiform, tightly constricted anteriorly, with a spinose shoulder, well developed axial ribs, and well differentiated, steeply rounded spiral cords (Figures 36–41), to trigonally fusiform, with only a moderate anterior constriction, a shoulder with low knobs, broadly rounded axial

ribs, and flattened, poorly differentiated spiral cords (Figures 42, 43, 46, 47). Some specimens show a diminishment of sculpture from the earliest whorls, where fluted spines occur at the shoulder of every axial rib, to the body whorl, on which shoulder spines and spiral sculpture are greatly reduced (Figures 48, 49).

The phylogenetic position of *Tactilispina* is unclear. The labral tooth emerging from the fifth spiral cord suggests an affinity with *Ocinebrellus* Jousseume, 1880, or *Muregina*. Supposing that *T. vermeiji* is a member of the *Muregina* clade, however, requires that (1) the labral tooth arose twice within the *Muregina* clade or that (2) taxa should be divided into a toothed lineage (late early Miocene to Recent, *T. vermeiji* and *M. lugubris*) and un-toothed lineage (early late Miocene to late Pliocene, *M. carlosmartini* and *M. marijkeae*). New material is needed to distinguish between these phylogenetic hypotheses or disprove both.

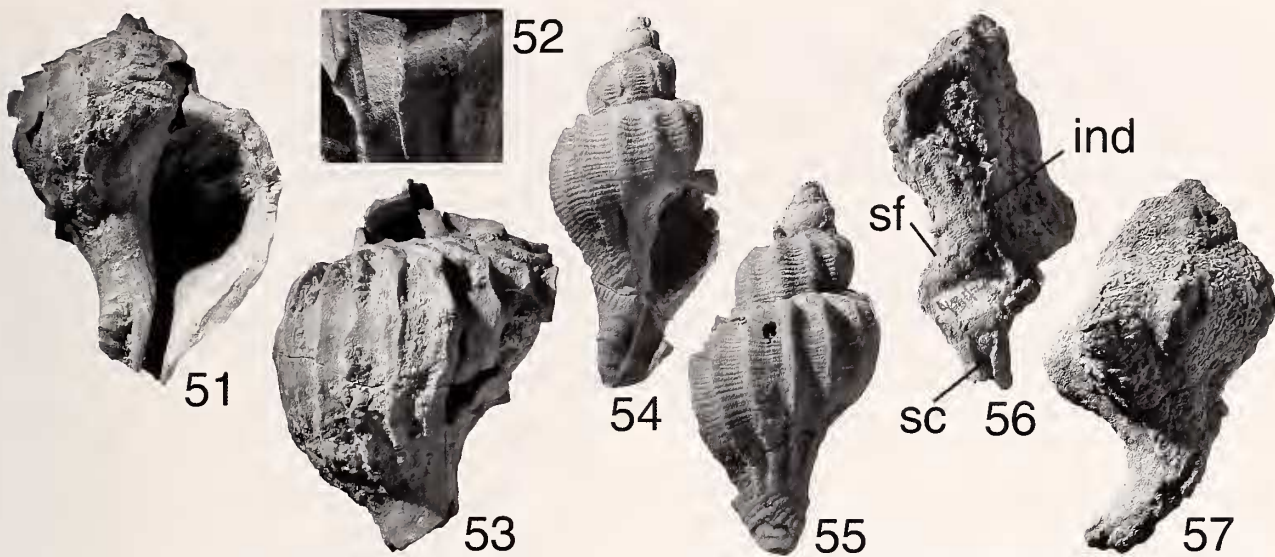
Specimens of *Tactilispina* superficially resemble those of species of *Ocinebrellus* Jousseume, 1880, especially some figured by Amano & Vermeij (1998) and Houart & Sirenko (2003; therein referred in many cases to *Ocenebra*). *Tactilispina*, however, has rounded axial ribs rather than flaring varices; rarely exhibits ribs with stacked growth lines facing adaperturally; never has a closed siphonal canal; always has a labral tooth; and has primary spiral cords that are either subequal in size or more strongly developed for the anteriormost two or three cords, only. The presence or absence of these features or their predominance are commonly used to distinguish ocenebrine genera (Vermeij, 1998; Vokes & Vermeij, 1998) and serve equally well to define *Tactilispina*.

Two Ecuadorian taxa bear some resemblance to *Tactilispina vermeiji*. *Trophon ecuadorius* Olsson, 1964, from the Pliocene 'Esmeraldas beds' of northwest Ecuador, was assigned to *Ocinebrellus* by Vokes (1988), who noted the presence of stacked laminae in the varices and a closed siphonal canal, and to *Muregina* by Vermeij (1998), who noted the absence of an adapical apertural sinus and abaperturally recurved spines on the axial ribs. The sum of characters for either genus, however, does not match that of *Tactilispina*. *Ceratostoma notiale* Vokes, 1988, also from the Pliocene 'Esmeraldas beds' of Ecuador, has four slightly flanged ribs on the body whorl, unlike *Tactilispina*.

Etymology: Named for the paleontologist Geerat Vermeij, who has added greatly to our understanding of the evolution of toothed gastropods.

Type locality: The lower flanks of eastern hills overlooking Quebrada Gramonal (locality-sample DV 1180-1) near its intersection with the Rio Ica (Figure 50).

Material: UWBM 97616, DV 1180-1, holotype, L (27.3), W 17.9; MUSM INV 060, DV 1180-1, paratype, L 29.4, W (17.6); MUSM INV 061, DV 1307-1, paratype,



Figures 51–53. *Xanthochorus cassidiformis* (Blainville, 1832). OSU 37546. Figure 51. Apertural view. Length is 47.5 mm. Figure 52. Close view of corrugated spiral threads. Figure 53. Abapertural view.

Figures 54, 55. *Trophon macharei*, sp. nov.. UWBM 97620. Holotype. Figure 54. Apertural view. Length is 37.9 mm. Figure 55. Abapertural view.

Figures 56, 57. *Phyllonotus* sp. indet. UWBM 97624. Figure 56. Apertural view, most of the right side is missing. ind—inductura, sf—siphonal fasciole, sc—siphonal canal. Length is 50.6 mm. Figure 57. Lateral view.

L (24.8), W 17.6; MUSM INV 062, DV 1021-3, paratype, L (23.5); MUSM INV 063, DV 1307-1, W 14.4; UWBM 97617, DV 1307-1, paratype, L 30.0, W 17.0; UWBM 97618, DV 1307-1, paratype, L 11.0, W (7.5); UWBM 97619, DV 1021-3, paratype, L 23.3, W (14.0). All latest early Miocene to early middle Miocene.

Occurrence: Uppermost lower Miocene to lower middle Miocene, southern Peru.

Subfamily Trophoninae Cossmann, 1910

Genus *Xanthochorus* Fischer, 1884

Type species: *Trophon xanthostoma* (Broderip, 1833) (synonym of *Xanthochorus cassidiformis* (Blainville, 1832)).

Xanthochorus cassidiformis (Blainville, 1832)

Figures 51–53

Purpura cassidiformis Blainville, 1832, p. 230 (also paginated as p. 42).

Xanthochorus cassidiformis (Blainville, 1832). DeVries, submitted, figures 3–12, 14, 16.

Xanthochorus cassidiformis var. *lamellosa*. DeVries, 1986, p. 589, pl. 37, fig. 9.

Discussion: This extremely lamellose example of *Xanthochorus cassidiformis* from Lower Pleistocene deposits of northern Peru resembles specimens of *Trophon geversianus* (Pallas, 1774). It is placed with *Xanthochorus*,

however, because its pattern of primary and secondary spiral cords is similar to that of many specimens of *Xanthochorus*, and because its tertiary spiral corrugations (Figure 52) have an identical texture to that seen on all specimens of *Xanthochorus* but not seen on specimens of *T. geversianus*.

Material: OSU 37546, DV 217-5, latest Pliocene or early Pleistocene, L (47.5), W 35.9.

Occurrence: Uppermost Pliocene or lowermost Pleistocene, northern Peru. Pleistocene to Recent, Ecuador to Chile.

Genus *Trophon* Montfort, 1810

Type species: *Murex magellanicus* Gmelin, 1791 (= *Buccinum geversianum* Pallas, 1774).

Trophon macharei, sp. nov.

Figures 54, 55

Diagnosis: Shell fusiform, turriculate, suture well below periphery of preceding whorl; axial sculpture of 14 low lamellae; spiral sculpture of about 45 rounded cords.

Description: Shell less than 40 mm long, fusiform, elongate; spire about 40 percent, siphonal canal about 20 percent of shell length. Protoconch unknown. Teleoconch with five whorls. Sutures impressed, attached well below periphery. Sutural platform tabulate, narrow; shoulder

nearly orthogonally angulate; periphery marked by slight swelling anterior to shoulder. Axial sculpture with 14 low, solid, evenly spaced lamellae on body whorl; axial ribs progressively fewer and less lamellose apically. Lamellae flattened at suture; maximally developed at shoulder; extended in diminishing strength to siphonal fasciole. Spiral sculpture of about 40 low, rounded, spiral cords between shoulder and siphonal fasciole, nearly all of equal strength; five additional spiral cords of comparable size on sutural platform; cords separated by v-shaped grooves. Aperture oval. Growth lines orthocone, outer lip and columella missing; siphonal canal open, straight, bent slightly to left but not dorsally. Siphonal fasciole weak, nearly parallel with siphonal canal; pseudumbilicus narrow, mostly obscured by adherent inner lip.

Discussion: With the outer lip and part of the columella missing, it cannot be determined with certainty that this specimen is more closely related to elongate modern austral trophonines such as *Trophon pelseneeri* E. A. Smith, 1915; *Trophon ohlini* Strebel, 1905; and *Trophon pallidus* (King & Broderip, 1832), than to species of Ocenebrinae. The lack of differentiated spiral cords, the absence of scabrous texture, and axial lamellae that are flattened at the sutures, however, characterize both *Trophon macharei* and modern South American trophonines.

Etymology: Named for José Macharé, Peruvian geologist who has worked closely with paleontologists to further our understanding of the tectonic history of the Pisco Basin.

Type locality: Roadcut along the Panamerican Highway on the north flank of the Yauca Valley (locality-sample DV 809-1), in a bioclastic sandstone below terrace deposits (Figure 26).

Material: UWBM 97620, DV 809-1, holotype, early Pliocene, L 37.9, W (18.0).

Occurrence: Lower Pliocene, southern Peru.

Subfamily MURICINAE Rafinesque, 1815

Genus *Phyllonotus* Swainson, 1833

Type species: *Murex imperialis* Swainson, 1833.

Phyllonotus, sp. indet.

Figures 56, 57

Discussion: Too little of this specimen is preserved to warrant a species name, but the remnants of an inductura and a siphonal canal that (1) is covered by a broad shelf to the left, (2) is narrowly open to the far right, and (3) is strongly recurved distally, suggest assignment to *Phyllonotus*. The specimen probably had about seven strongly developed axial varices, all lacking spines.

The tropical eastern Pacific Ocean is presently inhab-

ited by three species of *Phyllonotus* (Radwin & d'Attilio, 1976), two of which range southward into northern Peru. Fossil specimens of the spinose *Phyllonotus brassica* (Lamarck, 1822) occur in Pliocene beds of Ecuador (Pilsbry & Olsson, 1941; Olsson, 1964) and in uppermost Pliocene and middle Pleistocene beds of the Mancora and Talara tablazos of northern Peru (DeVries, 1986), while specimens of the non-spinose *P. globosus* (Emmons, 1858) were described from the Pliocene Esmeraldas beds of northwestern Ecuador (Vokes, 1988). This latest early Miocene fragment of *Phyllonotus* from the Ica Valley constitutes the southernmost and oldest occurrence of the genus in western South America.

Material: UWBM 97624, DV 484-6, late early Miocene, L 50.6, W (32.0).

Occurrence: Upper lower Miocene, southern Peru.

DISCUSSION

Toothed Muricids in Southern Peru

Tooth-bearing and non-tooth-bearing muricids from southern Peru since the early Miocene are listed in Table 1. Their numbers should be compared with Table 2 of Vermeij's (2001) survey of toothed gastropods. For nearly all sub-epochs there have been fewer muricids in the Pisco Basin than most regions globally, which has also been true for all mollusks (DeVries, 2002). Nevertheless, the numbers of toothed muricid species have been higher than numbers in most other regions, with their proportions consequently being among the highest worldwide. The proportions of toothed muricids in Peru were especially high during the early, middle, and late Miocene, when numbers of toothed Peruvian muricid species were reduced but the numbers of non-toothed muricid species were even more reduced.

Most of the toothed muricids belong to the genera *Acanthina*, *Chorus*, and *Hermineospina*. Two or perhaps all three genera may form a single clade (DeVries & Vermeij, 1997; Vermeij, 2001; DeVries, 2003). The three genera have been characterized by low rates of origination with the exception of an early Pliocene radiation within *Chorus*. Without the *Acanthina* clade *sensu* Vermeij (2001), proportions of toothed muricids in the southeast Pacific Ocean would be comparable to other regions of the world. Thus, the history of toothed taxa in the Peruvian Faunal Province is largely a history of the *Acanthina* clade—its appearance in the late Oligocene in the guise of *Acanthina katzi*, its radiation during the middle Miocene, and its near demise at the end of the Pliocene.

At the end of the Pliocene 80 percent of all mollusks disappeared or became extinct within the boundaries of the Peruvian Faunal Province (DeVries, 2001). Among early Pliocene toothed muricids in southern Peru, all species of *Chorus* became extinct and populations of a newly evolved species, the extant *Chorus giganteus* (Lesson, 1830), dis-

Table 1
Temporal distribution of muricids with and without a labral tooth in southern Peru.

Time Interval	Muricids without a Labral Tooth	Muricids with a Labral Tooth
Pleistocene to Recent	<i>Crassilabrum crassilabrum</i> <i>Stramonita biserialis</i> <i>Stramonita chocolata</i> <i>Xanthochorus buxea</i> ^a <i>Xanthochorus cassidiformis</i> ^a	<i>Acanthina unicornis</i> <i>Concholepas concholepas</i>
Late Pliocene	<i>Concholepas camerata</i> /C. <i>nodosa</i> ^b <i>Concholepas kieneri</i> <i>Crassilabrum crassilabrum</i> <i>Stramonita biserialis</i> <i>Stramonita chocolata</i> /spp. nov. <i>Xanthochorus buxea</i> <i>Xanthochorus cassidiformis</i> <i>Xanthochorus xuster</i> ^c	<i>Acanthina unicornis</i> /A. <i>triangularis</i> <i>Chorus blainvillei</i> <i>Chorus doliaris</i> <i>Chorus grandis</i> /C. <i>giganteus</i> <i>Herminespina mirabilis</i>
Early Pliocene	<i>Concholepas kieneri</i> <i>Concholepas nodosa</i> <i>Eupleura urbinai</i> <i>Muregina carlosmartini</i> <i>Purpura boliviana</i> <i>Stramonita biserialis</i> <i>Trophon macharei</i> <i>Xanthochorus eripepomus</i> <i>Xanthochorus ochuroma</i>	<i>Acanthina triangularis</i> /A. <i>obesa</i> <i>Chorus grandis</i> <i>Herminespina saskiae</i> /H. <i>philippi</i>
Late Miocene	<i>Concholepas kieneri</i> <i>Muregina carlosmartini</i> <i>Purpura boliviana</i> <i>Xanthochorus stephanicus</i>	<i>Acanthina obesa</i> <i>Acanthina rugosa</i> <i>Chorus frassinetti</i> <i>Herminespina philippi</i>
Middle Miocene	<i>Concholepas unguis</i>	<i>Acanthina katzi</i> <i>Tactilispina vermeiji</i>
Early Miocene	<i>Concholepas chirotenis</i> <i>Phyllonotus sp. indet.</i>	<i>Acanthina katzi</i> <i>Carluaspina comotrana</i>

^a Contrary to the original description and assignment of Vermeij (2001), *Xanthochorus cassidiformis* and *X. buxeus* are herein described as 'untoothed.' The labral tooth on fossil and modern specimens examined by the author are present sporadically, extend from different spiral cords on different specimens, and are weakly developed when present.

^b Pairs of ancestor-descendant species that span a time interval but have non-overlapping temporal ranges.

^c Bold-faced taxa have been described by the author. See text for citations.

appeared from southern Peru and became restricted to central and southern Chile (DeVries, 1997a). The only late Pliocene species of *Herminespina*, *H. mirabilis* (Möricke, 1896), became extinct (DeVries & Vermeij, 1997). *Acanthina* underwent a transformation from *A. triangularis* DeVries, 2003, to *A. unicornis* (Bruguère, 1789) and to a precursor of the modern southern Chilean-Argentinian species, *A. monodon* (Pallas, 1774) (DeVries, 2003).

Beyond the *Acanthina* clade, two early Pliocene untoothed rapanines, *Concholepas kieneri* Hupé, 1854 and *C. nodosa* Möricke, 1896, became extinct during the late Pliocene, but not before one gave rise to a toothed species, *C. camerata* DeVries, 2000, which in turn quickly evolved into the modern toothed *C. concholepas* (Bruguère, 1789) (DeVries, 2000).

Biogeography of Pisco Muricids

The geographic origin of known fossil muricids and easily discovered modern muricids from southern Peru

are listed in Table 2. Origins are inferred from the distribution of closely related taxa and, in the case of 'endemic' taxa, evidence of evolution within the southern modern Peruvian Faunal Province and lack of evidence for occurrences outside the region. Excluded from consideration are many *Thais* species and other muricids, fossil and Recent, whose populations from northern Peru occupy the southern portions of ranges that usually reach northward to Central America or Mexico.

The preponderance of endemic Cenozoic muricid species is evident from Table 2. In addition to toothed ocenebrines of the proposed *Acanthina* clade are the endemic lineages of *Xanthochorus* and *Concholepas*. Few taxa entered the region from north or south. The appearance of several Panamic species during the early Pliocene coincided with the arrival of Panamic species drawn from other molluscan groups and may reflect elevated temperatures along the Peruvian coast at that time (DeVries, 2001).

Table 2

Geographic origin of muricid species in southern Peru ordered by late Cenozoic time intervals. "Endemic" signifies an origin and distribution restricted for the most part to Peru and Chile.

Time Interval	Species	Geographic Origin	
Pleistocene to Recent	<i>Acanthina unicornis</i>	Endemic	
	<i>Concholepas concholepas</i>	Endemic^a	
	<i>Crassilabrum crassilabrum</i>	Endemic?	
	<i>Stramonita biserialis</i>		Panamic
	<i>Stramonita chocolata</i>	Endemic	
	<i>Xanthochorus buxea</i>	Endemic	
Late Pliocene	<i>Xanthochorus cassidiformis</i>	Endemic	
	<i>Acanthina/unicornis/A. triangularis</i>	Endemic	
	<i>Chorus blainvillei</i>	Endemic	
	<i>Chorus doliaris</i>	Endemic	
	<i>Chorus grandis/C. giganteus</i>	Endemic	
	<i>Concholepas camerata/C. nodosa</i>	Endemic	
	<i>Concholepas kieneri</i>	Endemic	
	<i>Crassilabrum crassilabrum</i>	Endemic?	
	<i>Herminepina mirabilis</i>	Endemic	
	<i>Stramonita biserialis</i>		Panamic
	<i>Stramonita chocolata/S. spp. nov.</i>	Endemic	
	<i>Xanthochorus buxea</i>	Endemic	
	<i>Xanthochorus cassidiformis</i>	Endemic	
<i>Xanthochorus xuster</i>	Endemic		
Early Pliocene	<i>Acanthina triangularis/A. obesa</i>	Endemic	
	<i>Chorus grandis</i>	Endemic	
	<i>Concholepas kieneri</i>	Endemic	
	<i>Concholepas nodosa</i>	Endemic	
	<i>Eupleura urbinai</i>		Panamic
	<i>Herminepina saskiae/H. philippi</i>	Endemic	
	<i>Muregina carlosmartini</i>		Panamic?
	<i>Purpura boliviana</i>		Panamic
	<i>Stramonita biserialis</i>		Panamic
	<i>Trophon macharei</i>		Magellanic
	<i>Xanthochorus eripepomus</i>	Endemic	
	<i>Xanthochorus ochuroma</i>	Endemic	
	Late Miocene	<i>Acanthina obesa</i>	Endemic
<i>Acanthina rugosa</i>		Endemic	
<i>Chorus frassinetti</i>		Endemic^b	
<i>Concholepas kieneri</i>		Endemic	
<i>Herminepina philippi</i>		Endemic^b	
<i>Muregina carlosmartini</i>			Panamic?
<i>Purpura boliviana</i>			Panamic
<i>Xanthochorus stephanicus</i>			Magellanic
Middle Miocene		<i>Acanthina katzi</i>	Endemic
	<i>Concholepas unguis</i>	Endemic	
	<i>Tactilispina vermeiji</i>		Panamic?
Early Miocene	<i>Acanthina katzi</i>	Endemic	
	<i>Carhuaspina comotrana</i>	Endemic^b	
	<i>Concholepas chirotensis</i>		?
	<i>Phyllonotus sp. indet.</i>		Panamic

^a Bold-faced origins represent first appearances; the designation continues through subsequent subepochs.

^b First appearances of these taxa may represent radiative events from an *Acanthina* ancestor.

The high degree of endemism among southern Peruvian muricids and generally small number of Panamic immigrants might be expected for a cool-water fauna partly isolated from nearby tropical waters by both coastal upwelling and an eastern boundary current flowing

equatorward. What is surprising is the lack of congruence between Peruvian and Chilean muricid faunas during the Miocene, especially considering the great faunal similarity during the Pliocene and Quaternary (DeVries, 2001). From old and new molluscan compendia (Hupé, 1854;

Philippi, 1887; Watters & Fleming, 1972; Tavera, 1979; DeVries & Frassinetti, 2003; Nielsen, 2003) there emerges only one early and middle Miocene muricid from Chile that also occurs in Peru: *Acanthina katzi*. The Miocene muricid fauna of central Chile, which includes the genera *Nucella* Röding, 1798; *Bedevea* Iredale, 1936; *Xymene* Iredale, 1915; *Xymenella* Finlay, 1927; as well as five new endemic genera and several species of *Trophon*, reveals strong austral roots (Nielsen, 2003) but bears almost no resemblance to the southern Peruvian fauna preserved 1500 km to the north. DeVries & Frassinetti (2003) suggested that the early and middle Miocene Chilean faunas evolved in warm waters and were separated by an oceanographic barrier from a fauna evolving in cooler waters upwelled along the southern Peruvian coast. Not until Chilean waters cooled during the late Miocene, they argued, did the barrier disintegrate and faunas between 13°S and 33°S intermingle.

CONCLUSIONS

With this paper, a treatment of the systematics and biogeography of Neogene muricids from southern Peru is nearly complete, lacking only a detailed analysis of the Pliocene evolution of *Stramonita*, *Purpura*, and the description of possible Miocene and Pliocene ocenebrines with subequal axial and spiral sculpture. Notable features of the Cenozoic Peruvian muricid fauna—low diversity, high endemism, numerous members of the toothed *Acanthina* clade, susceptibility to extinction at the end of the Pliocene—are ready for further analysis. Questions can be raised about the adaptive pressures responsible for the pace and manner of evolution within the well documented lineages of *Acanthina*, *Chorus*, *Concholepas*, *Hermineospina*, and *Xanthochorus*. The species that gave rise to *Acanthina* (Oligocene), *Concholepas* (early Miocene), and *Xanthochorus* (middle Miocene) remain to be discovered. Indisputable morphologically intermediate specimens uniting *Acanthina* with the genera *Chorus*, *Hermineospina*, and *Carhuaspina* have yet to be found. Finally, the changing ecological role of intertidal and shallow subtidal muricid predators in southern Peru throughout the Cenozoic and the impact of these muricids on the diversity and species composition of the entire invertebrate fauna has yet to be addressed.

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APPENDIX

Localities Cited

- DV 112 Terrace VI, Cerro El Huevo, overlooking Bahia San Juan, southern Peru. See DeVries (1986) for detailed map of terraces. Lower to middle Pleistocene.
- DV 191 Terrace near Hornitos, northern Chile, 60 km north of Antofagasta, Chile. Pliocene.
- DV 202 Surface of Mancora Tablazo, north side of Quebrada Honda, roadcut, 16 km northeast of Talara, 1163 km of Panamerican Highway (North) (circa 1980). Upper Pliocene to Lower Pleistocene.
- DV 211-21 Punta Lobitos, northern Peru, beach. Recent.
- DV 217-5 Paita, Peru, cliff of sedimentary rocks overlooking eastern end of port terminus, 4.3–4.5 m in section. See DeVries (1986) for more details. Upper Pliocene.
- DV 244-2 5 km south of El Alto, northern Peru, southernmost branch of Quebrada Taime, dissected hills above cliff face; continuous thin shelly sandstone bed in siltstone; Golf Course member, Taime formation. Upper Pliocene.
- DV 360-1 Sud-Sacaco, western end of ridge extending from Panamerican Highway; level 1 of 4 Nov–83 loc. 3, base of slope. 15°34'43"S, 74°43'17"W (Yauca 1:00,000 quadrangle). Pisco formation. Lower Pliocene.
- DV 361-5 Sud-Sacaco: northeastern end of depression near Panamerican Highway. 15°34'17"S,

- 74°43'26"W (Yauca 1:100,000 quadrangle). Pisco formation. Lower Pliocene.
- DV 361-10 Sud-Sacaco, northeastern edge of depression near Panamerican Highway. 15°34'17"S, 74°43'26"W (Yauca 1:100,000 quadrangle). Pisco formation. Lower Pliocene.
- DV 362-1 Sud-Sacaco, south end on southeastern face of depression near the Panamerican Highway. Indurated shell beds. (Yauca 1:100,000 quadrangle). Lower Pliocene.
- DV 396-14 Lomas Chilcatay, massive yellow sandstone in midst of white diatomaceous silty sandstones, 28 m in section. 14°11'42"S, 76°06'57"W (Punta Grande quadrangle, 1:100,000). Chilcatay formation. Lower Miocene.
- DV 399-1 Playa La Raya, Laguna Grande, shallow water on eastern side of lagoon. (Punta Grande 1:100,000 quadrangle). Recent.
- DV 465a-1 San Juan de Marcona—San Nicholas bridge, roadcut in terrace (San Juan 1:100,000 quadrangle). Upper Pleistocene.
- DV 468-1 Playa Yanyarina, about 22 km southeast of San Juan de Marcona. 15°27'S, 74°59'W (Acarí 1:100,000 quadrangle). Recent.
- DV 484-6 Second rock bed below Yesera de Amara. 14°35'38"S, 75°40'10"W (Lomitas: 100,000 quadrangle). Chilcatay/Pisco formation. Lower to middle Miocene.
- DV 769-1 Promontory of Cenozoic sedimentary rock on eastern side of abandoned San Juan—Lomas road. Ridge capped with Pleistocene terrace coquina. (San Juan 1:100,000 quadrangle). Middle Pleistocene.
- DV 809-1 Yauca, roadcut on western side of Panamerican Highway as it descends to valley floor. 15°39'49"S, 74°31'50"W (Yauca 1:100,000 quadrangle). Pisco formation. Lower Pliocene.
- DV 810-1 Above Quebrada Champeque, 15 km northwest of Chala, marine terrace deposit at 200 m. (Chala 1:100,000 quadrangle). Upper Pliocene.
- DV 923-1 About 0.5 km southeast of Monte Redondo, eastern side of Río Acarí, ridge inside shallow, small depression. 15°36'40"S, 74°38'02"W GPS (Yauca 1:100,000 quadrangle). Pisco formation. Lower Pliocene.
- DV 1021-3 Eastern side of Quebrada Gramonal, hillside above point where road to coast crosses from western to eastern side of quebrada; 44.6 m in section. 14°44'19"S, 75°31'02"W GPS (Lomitas 1:100,000 quadrangle). Pisco formation. Middle Miocene.
- DV 1029-1 Depression in plain above Playa de Yauca, west of Panamerican Highway, three beds of shells on flank of small pointed hill. 15°39'29"S, 74°35'08"W GPS (Chala 1:100,000 quadrangle). Pisco formation. Lower Pliocene.
- DV 1031-1 Morro Abra de los Chaparrinos, half way up section. 15°48'41"S, 74°21'18"W GPS (Chala 1:100,000 quadrangle). Upper Pliocene.
- DV 1180-1 Second rock layer from valley floor, foot of Yesera de Amara. 14°35'41"S, 75°40'14"W GPS (Lomitas 1:100,000 quadrangle). Chilcatay/Pisco formation. Lower to middle Miocene.
- DV 1230-1 Fourth white shell bank from base of outcrop, flanking basement knoll, east side Quebrada Riacheulo. 14°40'45"S, 75°29'20"W GPS (Palpa 1:100,000 quadrangle). Pisco formation. Lower upper Miocene.
- DV 1254-8 Morro Abra de los Chaparrinos. 15°53'25"S, 74°09'52"W GPS (Chala 1:100,000 quadrangle). Upper Pliocene.
- DV 1307-1 Bluff east of the mouth of Quebrada Gramonal, overlooking road to Fundo Santa Rosa. 14°45'48"S, 75°30'23"W GPS (Lomitas 1:100,000 quadrangle). Pisco formation. Middle Miocene.
- DV 1372-1 Rocky beach on northwestern side of Punta Lomas (Acarí 1:100,000 quadrangle). Recent.
- DV 1418-1 Eastern side Acarí Depression. 15°34'50"S, 74°36'59"W GPS (Yauca 1:100,000 quadrangle). Pisco formation. Upper Pliocene.